Conodonts from the Early Triassic microbialite of Guangxi (South China): implications for the definition of the base of the Triassic System

Brosse, Morgane ; Bucher, Hugo ; Bagherpour, Borhan ; Baud, Aymon ; Frisk, Åsa M ; Guodun, Kuang ; Goudemand, Nicolas

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Towards an evolutionary sound definition of 'recovery'?

In the Early Triassic community, 'biotic recovery' is one of the most commonly used terms and a recurring debate is whether the biotic recovery was prolonged in the aftermath of the end-Permian crisis. The problem with this debate is that 'recovery' is understood in different ways by different authors. The latest review about the pattern and tempo of the biotic recovery following the end-Permian mass extinction (EPME) was written by Chen and Benton (2012). Although Chen and Benton are well aware of definition issues with the term 'recovery' (Chen and Benton, 2012, p. 4), their paper still implicitly and alternatively adopts various definitions of 'recovery'. In these regards, their paper illustrates well the wandering of the current literature and this is the reason I am discussing it here. My intention is not to criticize Chen and Benton's paper per se but to draw our attention towards this pervading conceptual issue.

In their 2012 paper, Chen and Benton reviewed the latest results about the biotic recovery following the end-Permian mass extinction (EPME) and they concluded that Triassic ecosystems were rebuilt stepwise from low to high trophic levels. Many of us reacted strongly to that paper, especially to their figure 4 (Chen and Benton, 2012, p. 7) and their claim that "immediate post-extinction ecosystems in the Griesbachian-Dienerian show only the lowest trophic level" (Chen and Benton, 2012, p.7), that is, primary producers, which they equate to microbes. It is obvious (as mentioned several times by Chen and Benton) that many more groups and other trophic levels were represented during this earliest Triassic interval [e.g. ammonoids (Brayard et al., 2009) and conodonts (Orchard, 2007), some being predators presumably (Purnell, 1995); see also Scheyer et al., 2014].

Then, how can we reconcile their figure and claim with the asserted presence of other organisms during that interval? I shall assume that Chen and Benton (2012) implicitly considered a given trophic level to be present only if it has achieved full recovery. This, in turn, raises the issue of defining the term 'recovery' for a trophic level. One recurrent definition used by Chen and Benton (2012) for a group or a community is a low abundance, high diversity and high evenness of that community. Let us take over this definition and have a look again at the Griesbachian data. Where is the evidence for a high diversity and low evenness of microbial communities in the Griesbachian? How do we know that the lowest trophic level had already recovered? The short-lived dominance of microbes in the earliest Griesbachian could also suggest that the corresponding microbes were ‚disaster taxa'. The same question applies to the other trophic levels, which, following Chen and Benton, were added sequentially on top of one another. Chen and Benton's figure 4 demonstrates that they did not apply the same definition of 'recovery' consistently throughout their paper.

In fact, like Chen and Benton (2012) we all implicitly and alternatively adopt various definitions of 'recovery'. My intention here is to stress out our need for either a consensual definition of ‚recovery' or the global acceptance by our community that discussions about recovery should be better contextualized. Recovery of a species, of a supra-generic clade, of a community, of an ecosystem or of a trophic level may be defined and quantified in different and possibly contradicting ways. The granularity (spatial, temporal or ecological resolution) we choose for our studies may influence our definition and hence our conclusions about the tempo of recovery. Moreover, although the recovery of a particular taxonomic group can be easily defined in terms of, for instance, its specific diversity, defining the recovery of a complex system with many interacting constituents can be challenging.

A generic, maybe largely approved definition of 'recovery' is "the return to a previous state" (Chen and Benton, 2012, p.3). Yet, this definition does not specify what the 'state' of a clade or of an ecosystem should be. For a given taxon, the most used metric of its state of recovery is its morphological diversity. One could argue that the state of recovery is better characterized by a set of parameters such as diversity, size, and community evenness, as well as the spatial distribution thereof, that is, whether the corresponding recovery signature is observed locally or globally.

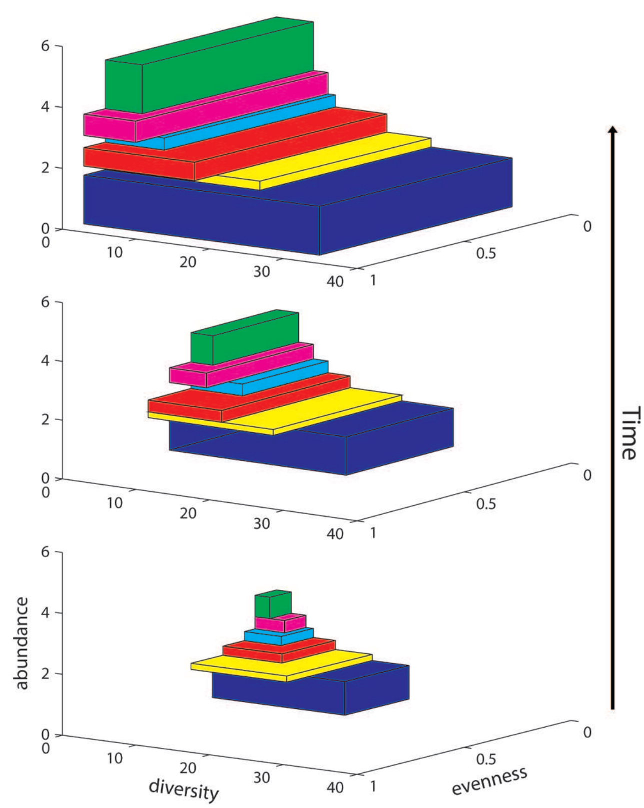

Figure 1 – Fictitious temporal evolution of an ecosystem's trophic pyramid during a recovery.

Yet, what is a good metric for the recovery of an ecosystem? Individual taxonomic groups show major differences in their response to the EPME: ammonoids thrived less than 2 myr after the EPME (Brayard et al., 2009) but corals are unknown from the fossil record until the Middle Triassic. Shall we compute an average of the groups' recoveries? Remember that some groups like the conodonts were positively affected (immediate recovery) and some groups like the trilobites never recovered. How can we appropriately describe the 'state' of an ecosystem?

The familiar way to understand recovery of a given system implies a relative stability (unity) of that system. If the system evolves too fast, we are not able to identify (a) normal, healthy state(s) in comparison with which we can define abnormal, crisis periods. The faster the system evolves in normal conditions, the shorter and tougher the crisis has to be in order for us to detect it and to define its boundaries. In other words, defining ecosystem descriptors that are less prone to variation is key for the identification of healthy steady states and crisis transitional phases.

Recently, Foster and Twitchett (2014) showed that there had been no loss of functional diversity of benthics through the EPME at the global scale. This is not surprising if one considers that the global structure of the network of ecological interactions within an ecosystem is likely to evolve much slower than its individual taxonomic groups: a given group of organisms may disappear but its ecological position or niche will eventually be filled by another group. Even if one expects the network of ecological interactions to co-evolve with the individual taxa, the relative stability of functional ecology makes it a better descriptor of the ecosystem than its ever-changing constitutive organisms. In these regards, Chen and Benton's suggestion (Chen and Benton, 2012) to using a trophic model of recovery for the EPME, a crisis that possibly lasted millions of years, is praiseworthy.

Let us assume that the shape of a particular trophic level is represented in three dimensions by, for instance, the abundance, diversity and evenness of the corresponding community. The state of the ecosystem is then described by a trophic pyramid, whose shape in this three- dimensional space is not necessarily a geometric pyramid (Fig. 1). Using this ecosystem descriptor, recovery could be defined as the restoration of a pre-crisis pyramid shape. As mentioned above, Chen and Benton's bottom-up restoration model is not supported by the data and it calls for a critical reappraisal. Alternative scenarios should be explored. For instance, the recovery trajectory may have instead involved a lateral expansion of the proposed trophic pyramid through increase of both diversity and evenness at all ecological levels (Fig. 1).

Besides the practical issues of identifying the ecological role of past organisms, in particular the role of taxa without extant analogs such as conodonts and ammonoids, one may argue that the term ‚recovery' sensu stricto implies that the post-crisis steady state (recovery state) is essentially the same as the pre-crisis state. Since the biosphere is likely to evolve drastically during major crises such as the EPME, it is not excluded that, when enough data is gathered, we have to recognize that the ecosystem did not, strictly speaking, recover from the EPME but went through what is called a critical transition: a transition from one equilibrium of the ecosystem to a new, distinct equilibrium.

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Nicolas Goudemand
Paleontological Institute and Museum, University of Zurich, nicolas.goudemand@pim.uzh.ch

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